THE ANATOMY
OF APHANODOMUS TEREBELLAE (LEVINSEN)
WITH REMARKS ON THE SEXUALITY
OF THE FAMILY XENOCOELOMIDAE NOV. FAM.

(Parasitic Copepoda)

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INTRODUCTION

Aphanodomus terebellae (Levinsen) is an extremely transformed and entirely internal copepod from arctic polychaetes. In spite of the great interest connected with this particular mode of life, no attempts have been made to examine the species more closely and it has until now remained very little known. The present paper contributes to the knowledge of its anatomy and systematic position ; in addition a discussion is given of some biological aspects, in particular of the nature of the sexuality of the species.

Since its first description, *Aphanodomus terebellae* has been recorded on several occasions (see table 1). The majority of the known specimens is deposited in the Zoological Museum of Copenhagen (nos. 1-6, 9, 11 and 12, table 1) and the account to follow is partly based on this relatively old material ; in addition, two rather newly formalin-preserved host-worms have been placed at our diposal through the courtesy of M. Pierre BRUNEL, Station biologique Marine, Grande Rivière, Gaspé, Québec (nos. 7 and 8, table 1). Dissections have been performed on a number of parasitized worms and in addition sectioning was carried out of parasites in situ. Of the Copenhagen collection we selected two parasitized worms for a microanatomical examination ; sectioning of the first (no. 5, table 1) failed completely, whereas that of the second (no. 6, table 1) succeeded surprisingly well and gave rise to a series of sections, in the following referred to as no. I. Section series were also made of one of the east Canadian specimens (no. 7, table 1) and are referred to as no. II. Paraffin-sections were cut 7-10 μ thick, and stained with iron haematoxylin and eosin, Masson's trichrome Stain, and Azan.

DISTRIBUTION

Aphanodomus terebellae has been recorded on 8 occasions from West Greenland (from Upernivik in the north to Bredefjord in the south) ;

there is a single record from South East Greeland, one from Iceland, one from the Kara Sea, and 2 from the Estuary and Gulf of St. Lawrence. An earlier record from Eastport, Maine (STEPHENSEN, 1913) was shown by LÜTZEN (1964 a) to be a mistake. Thus the occurrence of *Aphanodomus*, as so far known, is exclusively arctic (Fig. 1). A sample of almost 200 specimens of one of its hosts, *Thelepus cincinnatus*, from South Scandinavian waters (collected in the Gullmarfjord, northern Kattegat, and Oresund) has been examined, but no parasites were found.
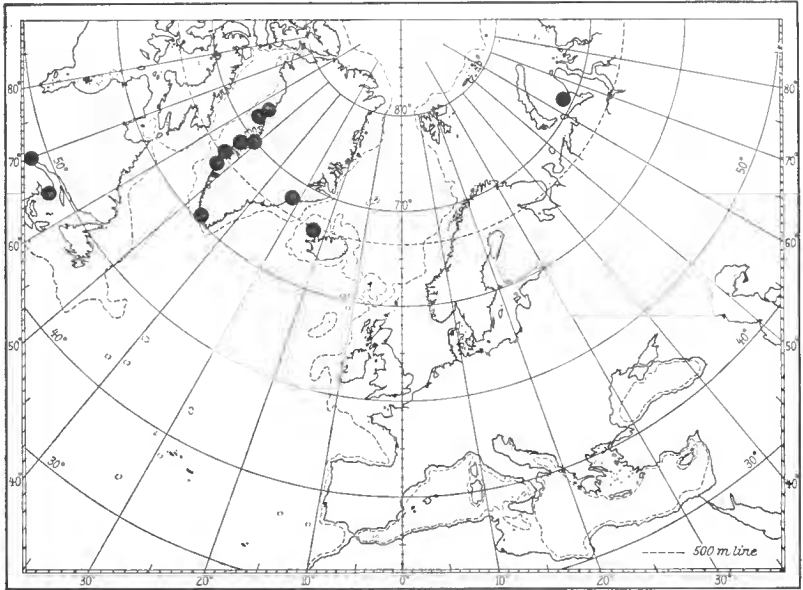

FIG. 1. — Distribution of *Aphanodomus terebellae* (Levinsen).

HOST AND LOCALIZATION ON THE HOST

As the accompanying table shows, 5 species of polychaetes belonging to 4 different genera have been recorded as hosts of *Aphanodomus*. This might be an indication that more than one species of *Aphanodomus* exists. To settle this question would certainly demand studies on the larval development and anatomy of parasites from all five hosts, since the number of external landmarks are very few. According to the view of P. Heegaard (quoted by WESENBERG-LUND, 1951) the parasite found on *Nicolea venustula* from Iceland is not identical with *A. terebellae*, although closely allied to it. On the other hand, dissection of the only other parasite of this host (from East Greenland) revealed many of the anatomical features peculiar to the parasite studied here, namely that of *Thelepus cincinnatus*. And as will appear later, the anatomy of

Table 1.

no.	locality	Host	number on host	first published by
1	Egedesminde, W. Greenland....................	*Amphitrite cirrata*..............	?	LEVINSEN (1878)
2	Kara Sea......................................	*Artacama proboscidea*...........	1	HANSEN (1886)
3	Sukkertoppen, W. Greenland...................	*Thelepus cincinnatus*...........	1	STEPHENSEN (1913)
4	Upernivik, W. Greenland......................	— —	5	STEPHENSEN (1913)
5	Holsteinsborg, W. Greenland..................	— —	2	HANSEN (1923)
6	Egedesminde, W. Greenland...................	— —	2	HANSEN (1923)
7	Saguenay Fjord, Québec.......................	— —	2	LÜTZEN (1964 a)
8	Grande Rivière, Gaspé, Québec...............	— —	2	LÜTZEN (1964 a)
9	Bredefjord, W. Greenland.....................	*Nicoloea zostericola*............	1	STEPHENSEN (1917)
10	Prøven, W. Greenland........................	— —	?	HANSEN (1923)
11	Kangerdlugssuak, E. Greenland................	*Nicolea venustula*..............	1	JESPERSEN (1939)
12	Isafjord, Iceland...............................	— —	1	WESENBERG-LUND (1951)
13	Ritenbenk, W. Greenland.....................	unknown.....................	?	HANSEN (1923)

the latter corresponds fairly well with the description given by LEVINSEN of the parasite from *Amphitrite cirrata*.

Only a few indications exist in the literature of the localization on the host. In the majority of instances, the parasite(s) were placed in the thoracal region, with the singular opening for the ovisacs piercing either the dorsal or ventral aspect. In one case (no. 11, table 1) it was placed in the 1st and 2nd abdominal segment, and in a second (no. 2, table 1) the position was obviously also abdominal. More than one parasite per host occur quite often, as appears from table 1, and LEVINSEN mentions that several parasites per host are found more frequently than single individuals, and reports on a host worm containing 19 parasites, of which 4 carried eggs.

As mentioned earlier, *Aphanodomus* is entirely internal. In live hosts, still quoting LEVINSEN, the parasite is recognizable from the outside as a light and somewhat transparent bulge of the skin. Otherwise it is recognizable on the host's surface only as a minute pore surrounded by a slight thickening of the polychaete's skin, through which the ovisacs are evacuated. If no ovisacs are present, the parasite is likely to be overlooked, and this might help to explain the fact that almost all collected specimens carried eggs.

The parasite adheres to the walls of the small pore but otherwise lies freely in the body cavity of its host. It does not adhere to the host's intestine as claimed by LEVINSEN ; this emerges clearly from dissections of the host and from a study of the section series. We never observed any parasites in a position like that figured by LEVINSEN (1878, pl. VI, fig. 19), that is with the longitudinal axis perpendicular to the antero-posterior axis of the host. All specimens dissected or sectioned by us showed an angle of 30-45º with this axis, or were lying parallel with it. In the case of 5 parasites in a single host (no. 4, table 1) 3 of these sat close together, side by side and the 4th a short distance from them.

EXTERNAL MORPHOLOGY

The body is without traces of segmentation. It is always oblong, and usually banana- or crescent-shaped with the concave side turned against the host's intestine. It may vary considerably, however, due to pressure from the surrounding host-organs and may exibit irregular constrictions or protrusions. The size is very considerable compared with other known copepod parasites from invertebrates ; the length is usually 6-8 mm compared with a maximum width of 2-3 mm ; in two cases length and maximal width were 11-12 and 4 mm respectively. Levinsen reports on a specimen which was 16 mm in length and 3-4 mm in diameter. The surface is finely wrinkled and there are no rudimentary appendages. In the central portion are found two opposed openings ; one of them, which in the following will be referred to as the atrioporus, is in continuity with the external pore and serves
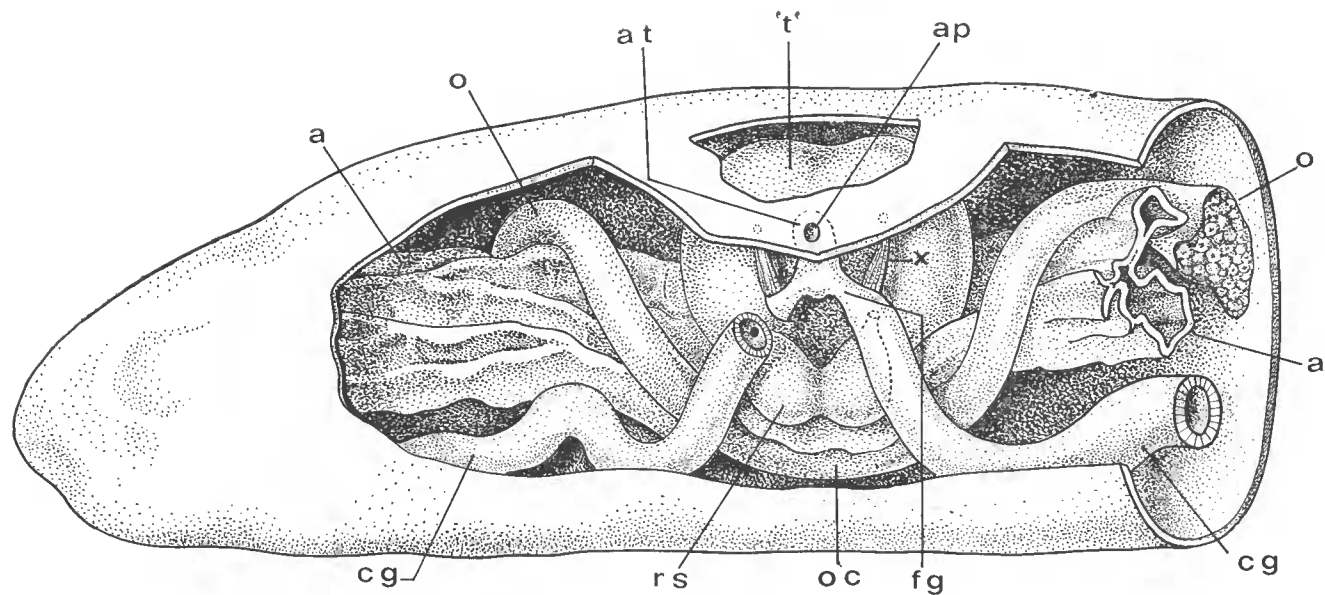
Fig. 2. — Stereogram of *Aphanodomus terebellae* (Levinsen) based on serial section I. Parts of the surface are removed to show the internal morphology. The female genital duct of one side is cut to show its communication with the receptaculum seminis.

a, axocoel; ap, atrioporus; at, atrium; cg, cement gland; fg, female genital duct; o, ovary; oc, communication between right and left ovary; rs, receptaculum seminis; 't', central vesicle containing spermatogonia; x, os uteri with muscular attachment.
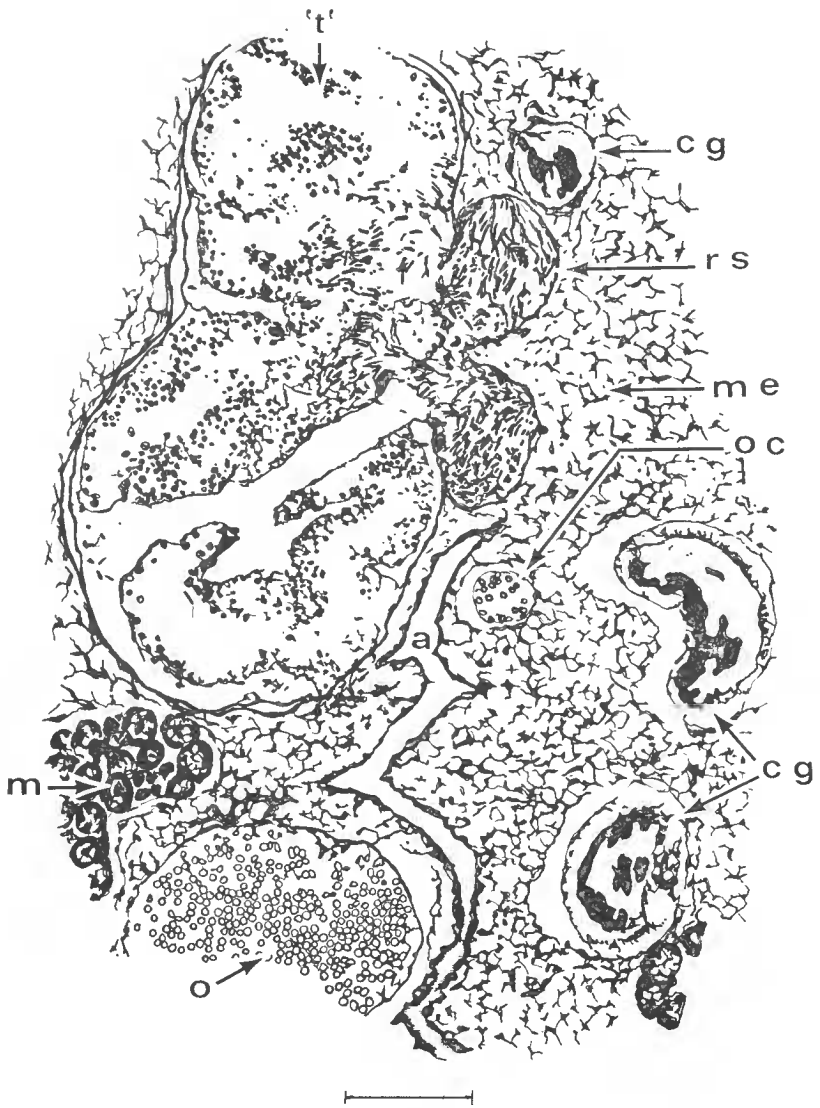
FIG. 3. — *Aphanodomus terebellae* (Levinsen).
Slightly oblique horizontal section (from serial section II).

a, axocoel ; cg, cement gland ; m, maturation-channel ; me, mesenchymatous tissue ; o, ovary ; oc, communication between right and left ovary ; rs, receptaculum seminis ; ' t ', central vesicle containing spermatogonia.

Scale represents 300 μ.

in the emission of the ovisacs. The other — or axoporus — leads into an interior cavity, the axocoel.

The median plane of *Aphanodomus* is easily established as a plane at a right angle to the longitudinal body axis through a line connecting the two body openings. The terms dorsal and ventral unfortunately cannot be used in the following description because of the impossibility of establishing the horizontal plane. The anatomy of *Aphanodomus* is rather simple. A true digestive system is absent, a nervous system is no longer demonstrable and a segmental muscular system does not exist. The interior is occupied by the voluminous reproductive organs and the above mentioned axocoel contained in a loose mesenchymatous tissue.

The axocoel communicates with the exterior, that is with the body cavity of the polychaete, through a narrow pore, the axoporus ; the axocoel is divided into symmetrical halves, right and left. It occupies almost the whole length of the parasite and reaches near to its tips. Its walls, as seen in sections, are collapsed, only leaving a very narrow space between them (Fig. 4) ; its central portion is a simple cleft, whereas the walls of the right and left halves show several, irregular ·ridge-shaped projections into the surrounding mesenchymatous tissue ; in sections perpendicular to the long axis of the parasite these projections are seen to radiate from a central tube of the axocoel. The walls of the axocoelic cavity are everywhere lined with a cuticle which at the mouth of the axoporus continues directly into the cuticle of the parasite's surface. The histological structure of the walls of the axocoel is very peculiar. The cuticle, which appears structurally homogenous, has a rather flat surface ; its thickness, however, varies very much due to the wavy course of the squamous epithelium which secretes it. Thus, membraneous areas alternate with others that show bugels into the surrounding mesenchyme (pl. 1, Fig. 1). The fact that the axocoel communicates with the coelomic cavity of the host makes it very probable that it contains coelomic fluid of the polychaete. Its function, therefore, is possibly mainly an absorptive one. LEVINSEN presumed it to be the parasite's intestine, but even if its function is that of an intestine it is at present impossible to say whether it is a homologue with part of the intestinal system or not. It might just as well have arisen as an invagination of the body surface and if so, a digestive system has become entirely lost in *Aphanodomus*.

The reproductive system consists of paired ovaries, a pair of cement glands, a bipartite receptaculum seminis and an unpaired, median vesicle containing spermatogonia and spermatocytes.

The ovaries lie on each side of the median vesicle one on the right, the other on the left. One of them was figured by LEVINSEN in this position (Pl. VI, Fig. 20, d) ; he described them as pear-shaped sacs containing a great number of spherical bodies of a yellowish colour, and
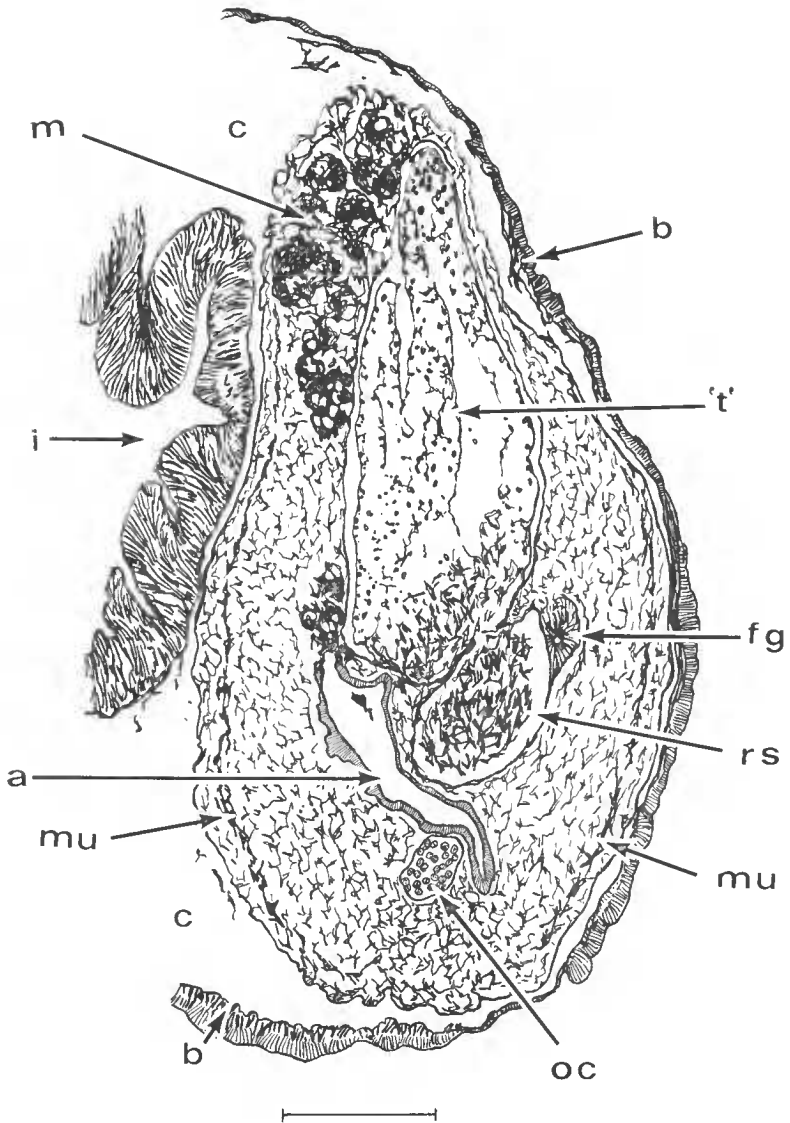
Fig. 4. — *Aphanodomus terebellae* (Levinsen).
Transversal section through median part of parasite in situ (from serial section I).

a, axocoel ; b, body wall of host ; c, coelomic cavity of host ; fg, female genital duct ;
i, intestine of host ; m, maturation-channels ; mu, sheet of striated muscular fibers ; oc,
communication between right and left ovary ; rs, receptaculum seminis ; ' t ', central
vesicle containing spermatogonia.

Scale represents 300 μ.

observed a number of milky-white winding tubules issuing from their lateral region ; he regarded these tubules as ovaries and was not able to interpret the nature of the two sacs. These are the true ovaries whereas the tubules are channel-shaped prolongations from the lateral portion of each ovary in which the maturation of the oocytes takes place. However, LEVINSEN's description of the relation of the tubules to the ovary was correct : laterally the ovaries diminish in size and break up into a small number of tubules which give off side-branches that might divide further. In the ovary proper, and in the tubules nearest to the ovary, oocytes are found with a diameter of less than 15 μ. In the remaining — and major — part of the maturation-channels the oocytes grow in size and become studded with yolk granules, until they reach a diameter of 90-100 μ. The largest oocytes occupy the center of the channels whereas the smaller one are displaced to the walls. The oocytes of the lateral parts of the ovaries are arranged in long, tightly packed rows that continue into the primary branches of the maturation-channels. After having issued from the ovaries some of the maturation-channels cross over to the opposite side of the axocoel. They spread all over in the mesenchymatous tissue in the lateral two-thirds or more of the parasite's left and right halves and are only absent from the mid-region.

The right and left ovary are mutually connected through a slender commissure containing oogonia and oocytes throughout its lenght. It usually shows a U-shaped course as appears from Fig. 2. Whereas the two ovaries are located on one side of the axocoel the communication between them is mainly lying on the other side.

The cement glands were also observed by LEVINSEN, although they were not recognized as such by him ; they appear on his Pl. VI, Fig. 20, as dark tubes issuing — as he claimed them to do — from the lateral part of the ovaries and crossing each other where they meet in the median line ; although these details are wrong the general course of the cement glands as it appears from his illustration is correct. They originate on the ovarial side of the axocoel and lateral, though very close, to the ovaries ; each of them proceeds almost to the tips of the body, where they turn around and cross over to the other side of the axocoel, now running in the opposite direction. On their course they cross the U-shaped ovarial commissure on their "interior" aspect (Fig. 2). They continue into very short and non-glandular genital ducts which open into each side of the so-called atrium that communicates with the exterior through the atrioporus. The cement glands have a winding course and hence are cut several times in horizontal sections (Figs. 2 and 3).

Mature eggs migrate from the maturation channels into the cement glands, but this was never observed in the sections, possibly because this process is restricted to a short time just prior to oviposition. The ovisacs, while they form, pass the atrium to emerge from the atrioporus. Proximally they are attached by means of conventional os uteri in the walls of the genital ducts ; there is little doubt that these represent the "two peculiar, flat, chitinous bodies" described and figured by LEVINSEN (Pl. VI, Fig. 20, f) although not recognized as os uteri by him.

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The atrium is lined with a cuticle continuous with that of the surface, from which it is probably derived as a simple invagination of the area encircling the genital openings. Thus, the apparent reduction to one of the two genital openings characteristic of other copepods is obviously secondary and certainly an adaptation to the internal nature of the parasitism in *Aphanodomus*. The dorsal and ventral walls of the atrial cavity show slit-like outpushings (not to be seen in Fig. 2), the function of which is obscure.

The unpaired, median vesicle was described by LEVINSEN (Pl. VI, Fig. 20, c) as an oval body containing a great number of small spherical corpuscles and " besides some long, whitish, vermiform, flat bodies ". The shape of the vesicle varies in the section series according to the section-direction and LEVINSEN's characterization is certainly fairly correct. On one side it communicates through a wide opening with the receptaculum seminis, which is a rather small bipartite body obviously not observed by LEVINSEN. The walls consist of a low epithelium with indistinct cell bodies but are otherwise sharply demarcated from the interior ; lining the whole cavity, except where it communicates with the receptaculum seminis, is a very thin, acellular membrane probably secreted by the epithelium. It does not everywhere stick to the epithelium but is here and there detached, possibly as a result of the sectioning procedure. It does not stain as a basement membrane, but on the other hand shows the same staining properties as does the exterior cuticle of the parasite. As a matter of fact it is almost indistinguishable from this cuticle although it is somewhat thinner. The vesicle encloses a very small number of irregularly shaped bodies, two of which are seen on the section in Fig. 3. It is reasonable to assume that these are the bodies which LEVINSEN found in the vesicle of freshly dissected parasites and which he stated to be long, whitish and vermiform ; on the old and rather badly preserved specimens at our disposal we have been unable to confirm his observations. The walls of the bodies are very thin and made up of an irregular layer of serpmatogonia ; the interior contains spermatocytes in all stages of spermiogenesis and comparatively few mature sperm cells. The walls show a few ruptures, especially in the region adjacent to the opening into the receptaculum seminis, and through these the sperm cells are seen to migrate into the right and left halves of the receptaculum to accumulate there. The mature sperm cells are whip-shaped, but since we have not observed them alive, we cannot state their exact lengths. However, judging from the sections, their lengths are considerable.

The two cement glands approach the receptaculum seminis from each side and eventually touch its lateral walls ; this is seen in Fig. 3, which shows a horizontal, but slightly oblique, section in which the cement gland of one side has come into contact with the receptaculum, though that of the other side has not done so yet. The receptaculum seminis is a double structure, being completely divided into a left and a right half by a median incision ; hence, it has two openings into the vesicle in which the sperm is produced , a right one, and a left one (Fig. 3).

Towards the other end each half of the receptaculum tapers into funnel-shaped duct that opens into the short female genital duct of the respective side just where the latter proceeds into the cement glands (Fig. 2).

Thus the function of the reproductive system of *Aphanodomus* is obvious : oocytes migrate into the maturation-channels and after having matured there enter the cement glands ; here they are embedded in a matrix secreted by the glandular walls and the ovisacs so formed are pushed through the cement glands. As they pass into the genital ducts the eggs become fertilized by sperm cells which have been stored in the receptaculum seminis.

All organ interspaces are filled by a loose meshwork of stellate mesenchyme cells (Fig. 3) in which neclei are hardly distinguishable. Striated muscle fibers form a continuous, but very thin sheet just beneath the body surface (Fig. 4) ; its fibers are mainly parallel with the surface and it is quite possible that one of its functions is to renew, by contraction, the content of body fluid present in the axocoel.

The body surface is somewhat wrinkled, which seems only partly to be due to sectioning. It is covered by a continuous cuticle, ca. 3 µ thick.

The systematic position of Aphanodomus.

The most distinctive characters of *Aphanodomus* are : the entire loss of segmentation and appendages ; withdrawal of the two genital openings into an invagination (atrium) obviously derived from the surface ; the presence of a central vesicular organ in which sperm cells are produced ; and the presence of a cuticularised cavity (axocoel) in continuity with the body surface. As far as we know, this combination of characters are found only in one other genus, namely *Xenocoeloma* Caullery & Mesnil.

Xenocoeloma contains two very close species, which according to the view of Bocquet, Bocquet-Védrine & L'Hardy (1965) are identical. It parasitizes the polychaete *Polycirrus* and appears as sausage-shaped projections from the host's body completely covered by the skin except for a single apical opening through which the ovisacs — if present — protrude. Its anatomy has been elaborately studied by Caullery & Mesnil (1919). Hansen (1923) shortly pointed to the possibility that *Aphanodomus* might be related to *Xenocoeloma* whereas Jespersen (1939) placed it in the family *Herpyllobiidae*. Unaware of Hansen's opinion, the present authors in 1960 suggested a relation to exist between *Aphanodomus* and *Xenocoeloma*, but not until now have we been able to discuss this matter further.

Although *Aphanodomus* and *Xenocoeloma* are quite dissimilar in external appearance, a comparison between them shows that they agree in anatomical respects point by point. Segmentation and appendages are lost in both. The ovisacs leave the body through an unpaired opening, the atrioporus, an almost unparalleled situation in parasitic copepods. In both there exists another opening, the axoporus, opposed

to the atrioporus and leading into a cavity which is unbranched and tubular in *Xenocoeloma*, and bipartite in *Aphanodomus*. This cavity, or axocoel, is lined with a thick cuticle in *Aphanodomus*, and is also cuticularised in *Xenocoeloma* according to the observation of BOCQUET et al. (l. c.), although cuticularisation was not observed by CAULLERY & MESNIL. The axoporus in both genera connects the body cavity of the host with the parasite's axocoel. In *Xenocoeloma* the latter is filled with coelomic fluid and this is supposed to be so in *Aphanodomus* also. The reproductive systems of the two genera are very similar : In *Xeno-coeloma* a left and a right ovary exist, connected through a short commu-nication, and the oocytes mature in maturation-channels. The French writers demonstrated spermatogonia and spermiogenesis in a large ovi-form vesicle comparable to the central, unpaired vesicle in *Aphanodomus* and on account of this claimed hermaphroditism to occur in *Xenocoeloma*. A minor disagreement between the two genera concerns the structure of the receptaculum seminis (' vésicule séminale ' of CAULLERY & MESNIL) which is entirely bipartite in *Aphanodomus* and undivided in *Xenocoe-loma*. In both genera, however, sperm are evacuated from the recep-tacle through paired ducts that open into the female genital ducts. Another difference is that *Aphanodomus* obviously lacks equivalents to the ' organe méandriforme ' and ' organe en rosette ' present in *Xeno-coeloma*. The arrangement of the striated musculature, in a single layer just beneath the skin, is similar in both ; and contrary to the statements of CAULLERY & MESNIL a cuticular covering of the body surface exists in *Xenocoeloma* as in *Aphanodomus* ; this has emerged from a recent study of the anatomy of the former by BOCQUET et al. (l. c.). Finally it should be mentioned that both genera are entirely internal parasites of poly-chaetes that all belong to the family *Terebellidae*.

We therefore suggest the establishment of a new family, the *Xeno-coelomidae*, to include *Xenocoeloma* Caullery & Mesnil and *Aphanodomus* Wilson. This family comprises internal parasitic copepods of poly-chaetes devoid of segmentation and appendages, with the genital openings withdrawn into an invaginated part of the surface that has a single ope-ning to the exterior ; with a centrally placed vesicle in which sperm cells are produced ; and with a tubular or bipartite cavity with cuticular walls and a single opening to the exterior, i. e. to the body cavity of the host.

It is at present impossible to say which of the two genera represents the most primitive condition. But it is fairly easy to convert one of them into the other by a shortening or lengthening of the axis between the axoporus and the atrioporus. This axis is very long in *Xenocoeloma*, and it is therefore natural that axocoel and cement glands are roughly parallel with it in this genus. In *Aphanodomus* it is very short and accordingly the cement glands have been turned to each side and the axocoel has spread in lateral directions.

The sexuality of the Family Xenocoelomidae.

Since its first description, *Xenocoeloma* has been considered to be a hermaphrodite, and this interpretation has been introduced into a number of handbooks without comment. We have earlier expressed doubts about the correctness of CAULLERY & MESNIL's conclusions (BRESCIANI & LÜTZEN, 1961, referred to also by BOCQUET & STOCK, 1963), and we
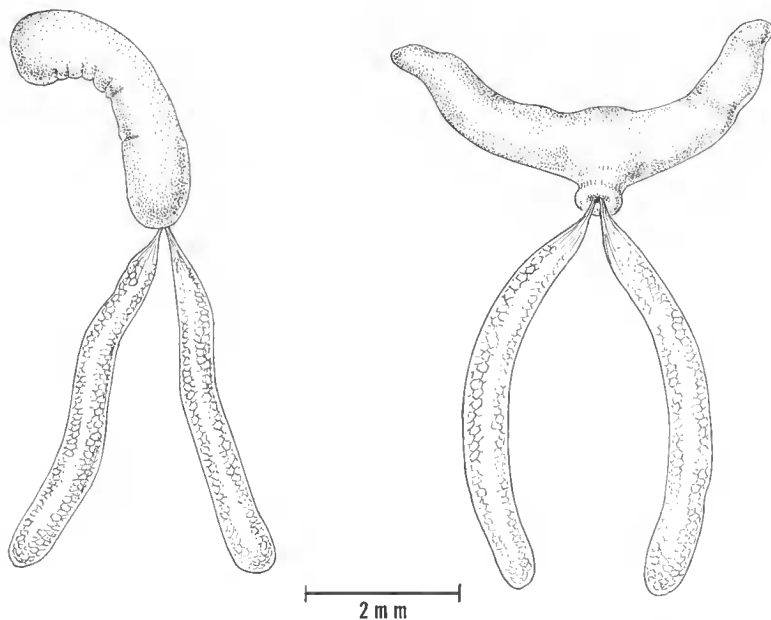

FIG. 5. — *Xenocoeloma brumpti* Caullery & Mesnil and *Aphanodomus terebellae* (Levinsen). Redrawn from BRESCIANI & LÜTZEN, 1960.

think this is a suitable opportunity to put forward in more detail an alternative explanation of the French writer's conclusions, even if we are not able to prove it conclusively. A short review of the following thoughts have been given elsewhere (LÜTZEN, 1964 *b*).

In our opinion neither *Xenocoeloma* nor *Aphanodomus* are true hermaphrodites. Our first argument concerns the relation between the female and ' male ' organs in the Xenocoelomidae and the development of the latter. As early as 1919 CAULLERY & MESNIL pointed to the fact that, among hermaphrodite crustaceans, Xenocoeloma was an exception because of the complete separatation of the male and female organs throughout life. Quoting CAULLERY & MESNIL (1919, p. 229) "*Xenocoeloma* se distingue, de la plupart des autres exemples d'hermaphro-
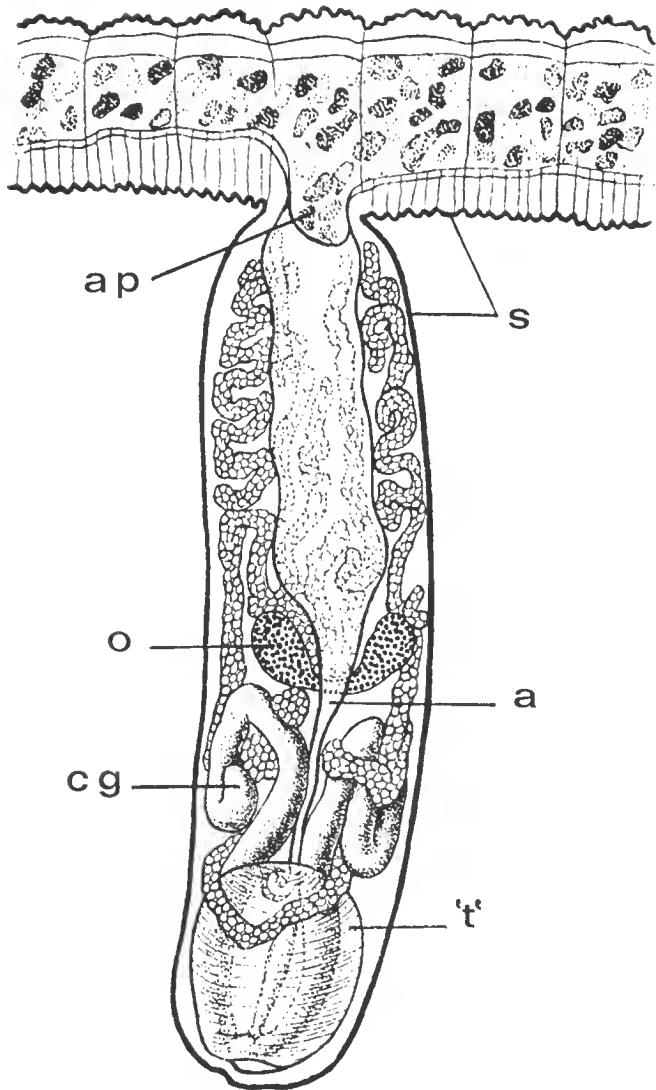
FIG. 6. — Anatomy of *Xenocoeloma brumpti* Caullery & Mesnil. From BAER, 1951.

a, axocoel ; ap, axoporus ; cg, cement gland ; o, ovary ; s, skin of the host ; ' t ', vesicle interpreted as testes by CAULLERY & MESNIL.

disme exceptionnel, par la façon dont cet hermaphrodisme est réalisé. En général, en effet, — et c'est le cas pour les Crustacés, tels que les Décapodes (Gebia major, Lysmata seticaudata, etc., etc.) ou les Isopodes (Cymothoadiens, Epicarides, Cryptonisciens, etc.), — c'est la glande génitale qui, d'unisexuée devient hermaphrodite, une partie de la glande évoluant en testicule, l'autre en ovaire et le plus souvent avec protandrie marquée ". As a matter of fact this seems to be a rule without exceptions in hermaphrodite crustaceans and has been supported by recent works on their sexual development (see for instance RUNNSTRÖM, 1925 ; REVERBERI & PITOTTI, 1942 ; and REVERBERI, 1947). In *Xenocoeloma*, however, again quoting CAULLERY & MESNIL, « le testicule se développe tout à fait en dehors de l'ovaire qui est la glande germinal typique, homologue de celle des autres Copépodes ».

We are still ignorant of the organogenesis in *Aphanodomus*. In *Xenocoeloma* the ovary and cement glands are already formed at a body length of 1 mm according to CAULLERY & MESNIL (1919), who studied a few young stages. At approximately this size the atrium comes into communication with the exterior by rupture of the polychaete skin that has hitherto covered its opening. The development of the so-called male organs ('testicule' and 'vésicule séminale' = receptaculum seminis of *Aphanodomus*) was observed to vary considerably in young parasites at a body length of 1 mm according to whether they were collected in the spring or in the autumn. CAULLERY & MESNIL described two of these stages. The first one, collected during the spring, shows a horizontal fissure ('fente testiculaire') with a cylindrical epithelium (CAULLERY & MESNIL, 1919, Fig. XVIII). At one end this fissure communicates with the atrium through a wide opening ; at the opposite end it is blind, and from each of its lateral walls emerges a narrow duct to end in the female genital duct of the respective side (see Fig. 7A). In the second stage, present in summer and autumn, is found a voluminous vesicle obviously derived from the above-mentioned fissure by constriction of its original communication with the exterior through the atrium (see Fig. 7B). The vesicle, which later develops into the 'testicule' of CAULLERY & MESNIL, opens into an adjoining cavity (the later 'vésicule séminale') which communicates with the genital ducts through the two above-mentioned ducts. At this stage spermatogonia form the walls of two vesicular bodies (CAULLERY & MESNIL, 1919, Pl. II, Fig. 15) that fill up entirely the lumen of the central vesicle. The two French writers state that these spermatogonia originate from a thickening of the wall of the central vesicle adjacent to the opening into the future 'vésicule séminale' ; in our opinion this has not been proved since intermediate stages showing this transformation do not exist ; one rather gets the impression that two distinct bodies dwell side by side in the common vesicle exactly as in the adult *Aphanodomus*, in which the median, unpaired vesicle seems to contain a small number of independant bodies with the walls composed of spermatogonia.

What is the nature of this central, unpaired vesicle containing the sexual products in both *Xenocoeloma* and *Aphanodomus* ? As shown

by CAULLERY & MESNIL, it communicates with the atrium, that is the exterior, during its rudimentary stage, but later this connexion breaks and it becomes entirely closed except for its opening into the future 'vésicule séminale'. Originally its rudiment may have arisen either as a fissure in the mesenchyme in stages prior to that figured in Fig. 7A, which for a short time obtains an open contact with the atrium ; or as an invagination from the atrium, that is from the body surface. There is reason to prefer the latter of these alternatives ; reference has been made earlier to the presence of an acellular membrane covering the walls of the median vesicle in the adult *Aphanodomus*, and it was found to have the same staining properties as the parasite's cuticle ; the membrane covered the entire vesicle, but stopped abruptly at the margin of the two openings into the receptaculum seminis ; it appears in Pl. 1, Fig. 2 as a thin sheet detached here and there from the epithelium which has secreted it. If it is true that this membrane represents the ordinary cuticle of the parasite, there is no doubt that the median vesicle in the xenocoelomids is an invaginated cavity derived from the body surface having lost entirely its connexion with the exterior ; this necessarily implies that the bodies made up of spermatogonia lying within it have been introduced from the exterior and that their origin are not to be sought in the parasite itself. But even if an ectodermal origin of the future sperm-producing vesicle is not accepted, the most reasonable explanation of the fact that it opens to the exterior at an early, prefunctional stage, is that in order to become functional it must receive something from outside.

We are inclined to believe that what is received are one or two very reduced dwarf-males in *Xenocoeloma*, possibly more in *Aphanodomus*. If so, each of the two bodies shown by CAULLERY & MESNIL (1919, Pl. II, Fig. 15) represents a male ; with age the male(s) increase their volume in time with the growth of the vesicle which contains them and eventually their true nature is hardly discernable. LEVINSEN, who seems to the only one who has dissected alive xenocoelomids, observed that the central vesicle in *Aphanodomus* contained " some long, whitish, vermiform, flat bodies ". These might have been the males, but unfortunately he did not report either on their number or size.

If the above explanation is true, the migration of males into the young parasites, which are then naturally females, happens at a body length of 1 mm ; according to CAULLERY & MESNIL's observations in the English Channel it must take place in the late spring or early summer, since young parasites collected in March had empty vesicles, whereas spermatogonia

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PLATE 1. — *Aphanodomus terebellae* (Levinsen). Scale represents 100 μ.

FIG. 1. — Detail of horizontal section to show the special structure of wall of the axocoel (serial section II).

a, axocoel ; m, maturation-channel ; o, ovary.

FIG. 2. — Detail of horizontal section to show the wall of the central vesicle (serial section II).

mc, mesenchymatous tissue ; sp, spermatogonia ; the arrow points at the membrane which stains as the parasite's cuticle.
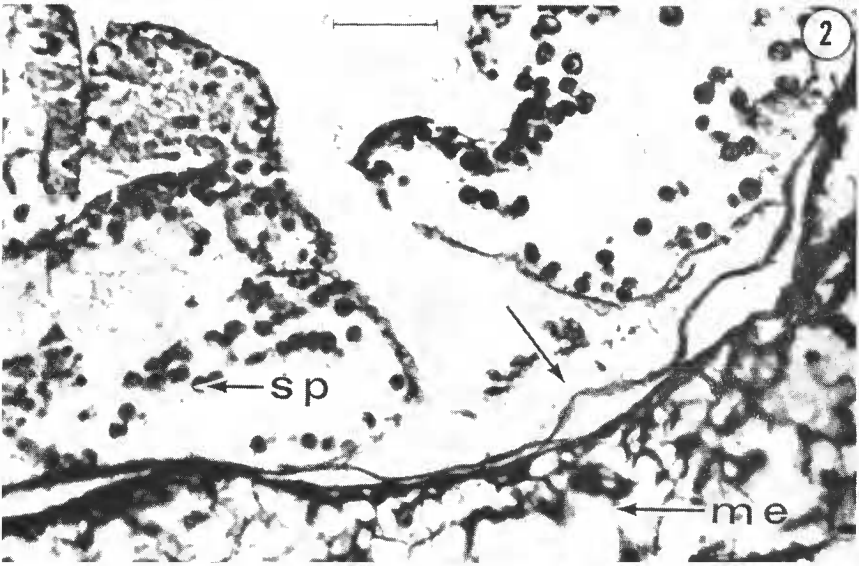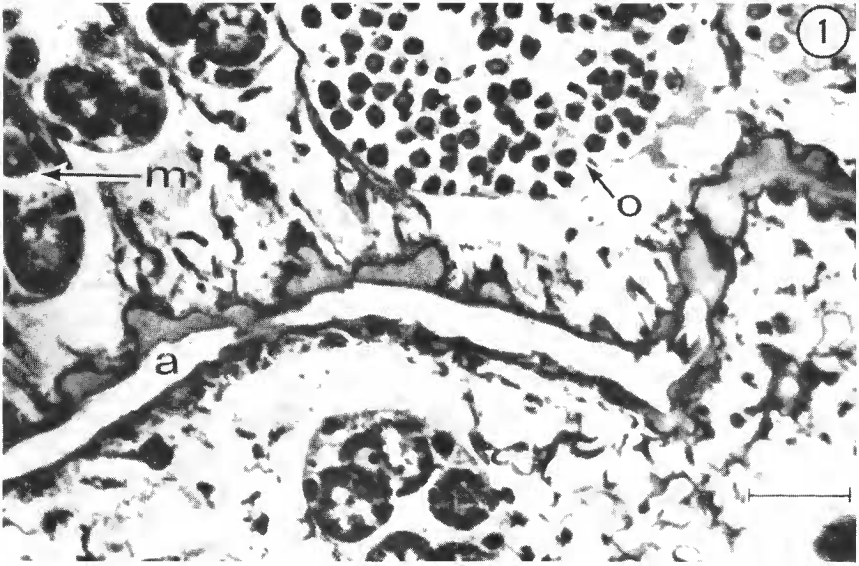
were present in those sampled during the summer and autumn. We may suppose that during this rather short period 1 or 2 dwarf-males, may be occasionally more, are attracted to the young female parasites and enter the atrium through the atrioporus, from there to find their way into the rudiment of the central vesicle. The connexion with the atrium is then sealed off and the males, now caught in the central vesicle, soon start spermiogenesis. On attaining maturity their walls rupture and sperm cells are evacuated through the opening into the receptaculum seminis (' vésicule séminale ').

The above interpretation of the sexuality in the xenocoelomids has a number of advantages above that hitherto accepted : It obviates the necessity for a concept of hermaphroditism among the copepods, *Xeno-*
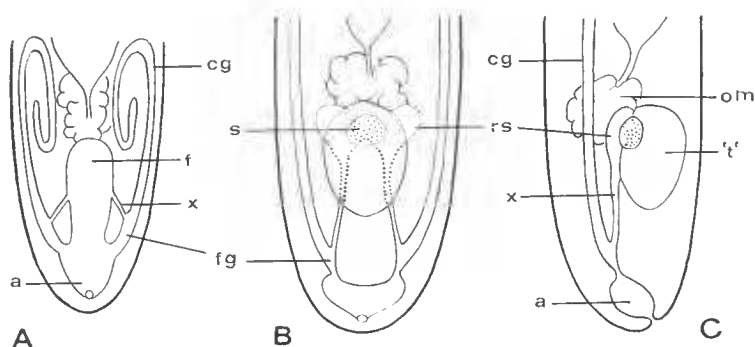

Fig. 7. — Organization of two young stages of *Xenocoeloma brumpti* Caullery & Mesnil ; A slightly younger than B & C (C viewed from the side). Redrawn from CAULLERY & MESNIL, 1919.

a, atrium ; cg, cement gland ; f, fissure probably arisen by invagination from the atrium (' fente testiculaire ' of C. & M.) ; om, meandriform organ ; s, region of proliferation of spermatogonia according to C. & M. ; ' t ', central vesicle ; x, duct comhining the receptaculum seminis (rs) and the female genital duct (fg).

coeloma having provided the only example of this, and it brings the sexuality of this genus on a par with that of all other copepods. It gives a satisfactory explanation of the independent origin of female and ' male ' constituents in the xenocoelomids ; and according to this interpretation *Xenocoeloma* and *Aphanodomus* are cross-fertilizers, whereas, if the theory of hermaphroditism is accepted, they would necessarily have to reproduce by compulsory self-fertilization, an exceedingly rare situation in the animal kingdom.

That the explanation put forward here is not only a theoretically possible alternative to that of CAULLERY & MESNIL, is evident from the present authors' studies on the sexuality of another parasitic copepod which in many ways presents a parallel to the xenocoelomids. *Gonophysema gullmarensis* Bresciani & Lützen, endoparasitic in the mantle of the ascidian *Ascidiella*, was first considered by us to be a hermaphrodite ; later, on studying its whole life-cycle, we were forced to revise this opi-

nion since the organ originally described as the testes by us turned out to be nothing but a cavity — derived from the exterior — containing a small number of reduced dwarf-males. The similarities with *Xenocoeloma* (and *Aphanodomus*) — for a discussion of these the reader is referred to our previous papers (1960, 1961) — are striking, but not necessarily indicative of a closer relationship. They might as well be understood as convergences acquired in connexion with the internal parasitic way of life.

It is a well-known fact that an extraordinary disproportion in size prevails between the sexes in a large number of parasitic copepods; the males are pygmys that usually dwell near the genital openings of the female. The evolutionary lines leading to *Xenocoeloma* and *Aphanodomus*, and *Gonophysema*, has been characterized by a steady decrease of the free body surface, and finally also the area of attachment for the males has been reduced in size. A possible way of compensating for this is to invaginate the female genital area to form a cavity for the reception of the males. Such an arrangement also has the advantage that it offers a better protection to the males. By deepening of the invagination the female genital openings eventually come to open into this cavity, and a typical atrium is formed whose opening is the only communication with the exterior. In *Gonophysema* this invagination has been divided, by constriction of its middle part, into an inner portion for incubating the males, and an outer one, the atrium, with a connexion between the two. However, the original continuity is interrupted in *Aphanodomus* and *Xenocoeloma*, and this may indicate a separate origin of *Gonophysema* and the *Xenocoelomidae* : In the former the male products are discharged into the female genital ducts via the atrium and from there reach the receptaculum seminis; this mode of introducing the male products directly into the female genital opening is likely to have been the usual condition in the ancestors of *Gonophysema*. The xenocoelomids seem to have departed from a type exemplified among recent copepods by the *Lernaeopodidae*, in which the sperm is discharged into the female genital ducts by way of two ducts from the surface. It may be argued, namely, that a receptaculum seminis comparable with that of *Gonophysema* does not exist in the *Xenocoelomidae*; the receptaculum of the latter might very well have arisen as dilation of the two ducts which are present in the young *Xenocoeloma* (Fig. 7A-C,x) ; the unpaired condition of the receptaculum seminis in this genus may have arisen secondarily as a union of these ducts for part of their length.

Hermaphroditism has been claimed also in *Flabellicola neapolitana*, since males were never found in a very large material of this copepod (GRAVIER, 1918). Absence of males has likewise been noted in a number of other parasitic copepods from polychaetes, viz. in *Phyllodicola* Delamare Debouteville & Laubier, *Cyclorhiza* Heegaard, *Bradophila* Levinsen, *Trophoniphila* McIntosh, and *Oestrella* McIntosh. It would be interesting to know whether this is accidental or whether a situation occurs in some of these species similar to that supposed by us to prevail in *Xenocoeloma* and *Aphanodomus*.

Résumé.

L'étude d'*Aphanodomus terebellae*, faite à partir de coupes sériées, a montré que le parasite est libre dans le coelome de son hôte. Une nouvelle famille, les *Xenocoelomidae*, est établie pour grouper les genres *Aphanodomus* et *Xenocoeloma*.

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REFERENCES

BAER, J. G., 1951. — Ecology of animal parasites. Univ. Illinois Press.

BOCQUET, C., BOCQUET-VÉDRINE, J. & L'HARDY, J.-P., 1965. — Sur la redécouverte, à Roscoff, de *Xenocoloma alleni* (Brumpt) et sur l'existence d'un tégument propre, indépendant de celui de l'hôte : *Polycirrus caliendrum* Claparède, chez ce Copépode parasite. *Bull. Mus. Nat. Hist. Nat.* Paris, **36**, pp. 622-625.

BOCQUET, C. & STOCK, J., 1963. — Some recent trends in work on parasitic copepods. Oceanography and Marine Biology, **1**, pp. 289-300.

BRESCIANI, J., 1964. — The anatomy of *Aphanodomus terebellae*, a parasitic copepod of terebellid polychaetes. Paper presented to the *1st Intern. Congr. Parasitology*, Rome, Sept. 1964.

BRESCIANI, J. & LÜTZEN, J., 1960. — *Gonophysema gullmarensis* (Copepoda parasitica). I, Anatomy. *Cah. Biol. Mar.*, **1**, pp. 157-184.

— — 1961. — *Gonophysema gullmarensis* (Copepoda parasitica). II, Biology and development. *Ibid.*, **2**, pp. 347-371.

BRUMPT, E., 1897. — Sur un copépode nouveau (*Saccopsis alleni*, n. sp.), parasite de *Polycirrus aurantiacus*. *C. R. Acad. Sci.*, Paris, **124**, pp. 1464-1467.

CAULLERY, M. & MESNIL, F., 1915. — Sur la structure et les rapports avec l'hôte (*Polycirrus arenivorus* Caull.) d'un Copépode parasite (*Xenocoeloma Brumpti* n. g., n. sp.). *Ibid.*, **161**, pp. 709-712.

— — 1917. — Nouvelles recherches sur *Xenocoeloma brumpti* C. et M. *Bull. Soc. Zool. France*, **42**, pp. 169-178.

— — 1918. — Phases parasitaires initiales du *Xenocoeloma brumpti*. *C. R. Acad. Sci.*, Paris, **167**, pp. 964-966.

— — 1919. — *Xenocoeloma brumpti* C. et M. Copépode parasite de *Polycirrus arenivorus* C. *Bull. Biol. France Belg.*, **53**, pp. 161-233.

GRAVIER, C. J., 1918. — Contribution à l'étude d'un Copépode (*Flabellicola neapolitana* Gravier) parasite d'un Annélide Polychète (*Flabelligera (Siphonostoma) diplochaitos* (Otto)). *Pubbl. Staz. zool. Napoli*, **2**, pp. 209-222.

HANSEN, H. J., 1887. — Oversigt over de paa Dijmphna-Togtet indsamlede Krebsdyr. Dijmphna-Togtets zool.-bot. Udbytte. Kjøbenhavn (Copenhagen), pp. 183-286.

— 1923. — Crustacea Copepoda. II, Copepoda Parasita and Hemiparasita. *Dan. Ingolf-Exped.*, **3** (7), pp. 1-92.

JESPERSEN, P., 1939. — The Zoology of East Greenland. III, Copepods. *Medd. Grønland*, **121** (3), pp. 1-66.

LEVINSEN, G. M. R., 1878. — Om nogle parasitiske Krebsdyr, der snylter hos Annelider. *Vidensk. Medd. Dansk naturh. Foren., Kbhvn.*, 1877-1878, pp. 351-380.

LÜTZEN, J., 1964 *a*. — Parasitic copepods from marine polychaetes of eastern North America. *Nat. cand.*, **91** (Trav. Pêch. Québec, no. 7).

— 1964 *b*. — The type of sexuality in *Gonophysema*, *Aphanodomus* and *Xenocoeloma* (parasitic copepods of invertebrates). Paper presented to the *1st Intern Congr. Parasitology*, Rome, Sept. 1964.

REVERBERI, G., 1947. — Ancora sulla trasformazione sperimentale del sesso nei Bopiridi. La trasformazione delle femmine giovanili in maschi. *Pubbl. Staz. Zool. Napoli*, **21**, pp. 81-91.

— & PITOTTI, M., 1942. — Il ciclo biologico e la determinazione fenotipica del sesso di *Ione thoracica* Montagu, Bopiride parassita di *Callianassa laticauda* Otto. *Ibid.*, **19**, pp. 111-184.

RUNNSTRÖM, S., 1925. — Beiträg zur Kenntnis einiger Hermafroditischen Decapoden Crustaceen. *Bergens Mus. Skr., Ny Række*, **3** (2).

STEPHENSEN, K., 1913. — Grønlands Krebsdyr og Pycnogonider. *Medd. Grønland*, **22**, pp. 1-479.

— 1917. — Zoogeographical investigations of certain fjords in southern Greenland, with special reference to Crustacea, Pycnogonida and Echinodermata. *Ibid.*, **53** (3), pp. 229-378.

WESENBERG-LUND, E., 1951. — Polychaeta. *The Zoology of Iceland*, II (19), pp. 1-182.

— 1953. — The Zoology of East Greenland. Polychaeta. *Medd. Grønland*, **122** (3), pp. 1-169.

WILSON, C. B., 1924. — New North American Parasitic Copepods, new hosts, and Notes on Copepod Nomenclature. *Proc. U. S. Nat. Mus.*, **64**, art. 17, pp. 1-22.